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MALE AGGRESSIVE BEHAVIOR IN A PAIR OF SYMPATRIC SIBLING SPECIES

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ABSTRACT. Intraspecific encounters were staged between adult male *Anolis marcanoi* and *A. cybotes* in order to describe their aggressive behavior. The major component of stationary behavior is the dewlap display, accompanied by various static and dynamic modifiers. Advancing behaviors include moving toward an opponent, threatening attack, and actual biting. The aggressive behavior of *A. marcanoi* is progressive and hierarchically structured. By contrast, the behavior of *A. cybotes* is less elaborate and ritualized than that of its sibling and lacks progressive structure.

INTRODUCTION

Defined simply as "pairs or even larger groups of related species which are so similar that they are considered as belonging to one species until a more satisfactory analysis clears up this mistake," (Mayr, 1942) sibling species have been discovered at an increasing pace as the level of systematic analysis has become finer, passing from examinations of morphological characters to investigations of molecular properties.

The different patterns of distribution of sibling species raise interesting ecological questions. On one hand, sibling species may be completely allopatric, which raises questions more about the evolutionary forces operating to produce such species than about the

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ecological relationships between them. On the other hand, parapatric and sympatric sibling species distributions bear directly on ecological theory. In theory, two species occupying the same niche cannot long coexist unless differences sufficient to lessen competitive pressures evolve. The parapatric ranges of many sibling species pairs or groups attest to the difficulty such species have in coexisting (e.g., the members of the *Rana pipiens* complex in North America [Pace, 1974] and the *Anolis chlorocyanus* [Williams, 1965] and *A. ricordii* [Schwartz, 1974] groups in Hispaniola). One would expect that sympatric sibling species would exhibit differences in morphology, physiology, or behavior that would permit coexistence. Indeed, resource partitioning of some kind is observed in almost all known cases of sympatric sibling species (Mayr, 1942; Schoener, 1977).

In this regard, the curious case of the Hispaniolan sibling species *Anolis cybotes* and *A. marcanoi* warrants attention. *Anolis cybotes*, the larger of the two, is found throughout the island, while *A. marcanoi* is restricted to a small area in the southwest portion of the Dominican Republic (Williams, 1975). The two are classic sibling species, consistently separable morphologically only by the color of the dewlap of males and the throat of females: *Anolis marcanoi* has a red dewlap or throat, while that of *A. cybotes* is usually either white or yellow, depending on locality (Williams, 1975). Electrophoretic studies by Webster (1975), however, clearly reveal that the two are distinct species. Table 1 provides a review of differences between the species.

Ecologically, the species are just as similar. Unlike the cases of sibling species already discussed, no apparent differences in physiology or microhabitat preference have been discovered. They are patchily sympatric throughout the range of *A. marcanoi* and have been noted on adjacent fenceposts in some areas (Hertz, 1980), while in other locations only one species is present. Hertz suggests that *A. marcanoi* may be better adapted for hotter, more open microhabitats, but no consistent differences have been noted in the field (Williams, 1975; Hertz, 1980; personal observation).

At issue is the manner in which these species interact. Are the differences between the species in dewlap color sufficient to allow species recognition, or are there also behavioral differences of importance? If species recognition is highly accurate, do the similar-

Table 1. Differences between *Anolis marcanoi* and *Anolis cybotes*.*

	<i>A. cybotes</i>	<i>A. marcanoi</i>
range	widespread throughout Hispaniola	Peravia Province, south-west Dominican Republic
dewlap color	normally white to yellow, except some populations on the extreme end of the southwestern peninsula in Haiti, which are red	red
scale characters	middorsal and midsacral scales sometimes enlarged	middorsal and midsacral scales rarely enlarged
maximum snout-vent length	81 mm	65 mm
heat tolerance:		
Experimental	34.3° C	35.7° C
Voluntary		
Maximum		
Critical Thermal	38.4° C	40.5° C
Maximum		

*After Williams, 1975 and Hertz, 1980.

ities between the species lead to resource competition and interspecific aggression? The goal of this study is to provide a thorough description of intraspecific male aggressive behavior in the two species. In themselves, reports on the intraspecific male aggressive behavior of both species are important because detailed characterizations of the components and progression of male aggressive behavior in *Anolis* are not common (the only reports of comparable detail are Greenberg and Noble, 1944, and Greenberg, 1977, on *A. carolinensis* and Jenssen 1979a and 1979b on *A. opalinus*). Furthermore, in order to analyze interspecific interactions, it is first necessary to understand the dynamics of intraspecific behavior. This knowledge then may be used as a control with which interspecific aggressive behavior can be compared.

MATERIALS AND METHODS

In January 1983, adult male *A. marcanoi* were collected past the first ford on the El Recodo road, approximately 6 to 10 km north of

Bani, Peravia Province, Dominican Republic. Adult *A. cybotes* were collected at that locality and in Santo Domingo, Dominican Republic. The lizards were housed in terraria in the Biological Laboratories, Harvard University, and provided with perches, small potted plants, and a soil substrate, and offered several crickets one to two times a week and water three to four times a week. Room temperature was maintained at approximately 26 to 30°C. Individuals were separated from other males in the same terrarium by cardboard partitions.

Encounters between two conspecific males were staged between 23 March and 16 December 1983. Lizards were placed in the partitioned halves of either a 41 × 22 × 20 cm (the first 14 *A. marcanoi* encounters) or a 74 × 32 × 29 glass terrarium (the last 12 *A. marcanoi* and all 19 *A. cybotes* encounters) covered with a mesh lid and provided with perches in each half of the terrarium. Lizards were left undisturbed in the terrarium for a period ranging from 17 hours to four days, but usually lasting two days. Water was only provided when an encounter had to be postponed, forcing the period to exceed two days. Lizards were allowed to acclimate in order to gain familiarity and enhance territorial defense.

Approximately 15 to 30 minutes prior to an encounter, a 250 W infrared light was switched on, warming the terrarium to 25 to 32°C and markedly increasing the activity level of the lizards. Temperature in the room in which the encounters were staged was approximately 20°C.

Encounters were initiated by lifting the partition. All lights in the room were extinguished, except two 60 W desk lamps pointed directly into the terrarium which lit the display arena and made it difficult for the lizards to see observers in the room. Encounters were videotaped on a Panasonic NV-8050 time lapse recorder with a MTI-65 video camera and a Canon 16-100 mm TV zoom lens and then analyzed at normal and slow-motion speeds on a Panasonic WV-5350 video monitor. Encounters normally lasted 45 minutes, but were terminated when one lizard tried repeatedly to escape from the other, and were extended when the lizards were still intensely interacting at the end of the allotted time.

Twenty-one *A. marcanoi* and ten *A. cybotes* were used in these encounters. Lizards were paired randomly, with the constraints that they had not been housed in the same terrarium, that they had no

prior experience with each other (two exceptions), and that there was no more than a 5 mm difference in snout-vent-length.

RESULTS

The aggressive behavior of the lizards can be divided into two categories: stationary and advancing behavior. In stationary behavior, the lizard remains in one area and primarily moves its head, bobbing with or without extension of the dewlap. Several modifiers of this display, either morphological changes or movements of body parts, are correlated with aggressive intensity, particularly in *A. marcanoi*. The level of intensity of *A. marcanoi* could be judged by the correlated appearance of behavioral and morphological responses. As displays progressed, lizards generally displayed a sequence of actions and display modifiers, adopted a more threatening posture with body and head raised and apparent size maximized, and became more active. By contrast, in *A. cybotes* there was little correlation between the appearance of particular aspects of aggressive behavior. Thus, level of intensity was more difficult to gauge.

In advancing behavior, the lizard moves toward its opponent. In the early, less intense stages, the lizard makes various intention movements, while later stages involve lunging and biting.

The male aggressive behavior of the two species differed in two major respects. First, though elements of both stationary and advancing behavior were displayed by *A. cybotes*, many of the components of these behaviors were absent or much less elaborate than those exhibited by *A. marcanoi*. Second, the ordered appearance of progressively more aggressive behaviors, so integral a part of male-male interactions of *A. marcanoi*, was absent in the behavior of *A. cybotes*. In most cases, particularly among stationary behaviors, any particular behavior did not necessarily follow any other particular behavior, nor did particular behaviors connote different levels of aggression.

Stationary Behavior

The primary stationary display of the lizards was the dewlap display, composed mainly of head-bobbing and dewlap extension.

Dewlap Display

Anolis marcanoi

There were generally three levels of intensity of the display exhibited by *A. marcanoi*. Intensity is best correlated with the degree to which the lizard elevated its body above the substrate.

The *low level dewlap display*, often the first display the lizard would make in an encounter, involved little body elevation. The body occasionally remained completely in contact with the substrate, but usually the anterior portion of the body was slightly lifted by extending the front limbs, holding them out to the side in the typical reptilian stance (Fig. 1a). The result was that the forequarters were raised several mm off the substrate. The snout was also angled upward at 30 to 45 degrees to the ground. The head usually was kept in the vertical plane of the body. During the process of raising the body and snout, the dewlap usually was extended completely with several rapid head bobs. On a number of occasions, the forebody distinctly raised first, and then the dewlap extended, but the two usually occurred simultaneously.

This display occurred primarily at the start of an encounter, shortly after the partition had been raised, though sometimes it was omitted altogether. Occasionally, when an encounter had proven indecisive and the lizards had calmed, they would revert to this level.

The *intermediate dewlap display* involved an increase in body elevation. Generally, it took one of two forms: either the forelimbs were completely extended with the snout pointed at a very high angle (75 to 90 degrees), giving the whole body a very steeply sloped configuration, or all four legs pushed up, with the hind legs out to the side, elevating the whole body off the substrate (Fig. 1b). The tail was then usually also lifted, either held rigid and completely elevated, or slightly arched with the posterior half dropping to the substrate. The tail was also on occasion held higher than the body or was even curled back above it. The dewlap was extended completely in this display; the snout's higher angle and the higher elevation of the forequarters (at least a little higher in the second variation than in the low level dewlap display) allowed the dewlap to be lifted completely off the substrate.

In the highest level of intensity display, clearly distinct from the first two, the entire body was elevated high off the substrate (Fig. 1c). In the *full elevation display*, the forelimbs were held under the

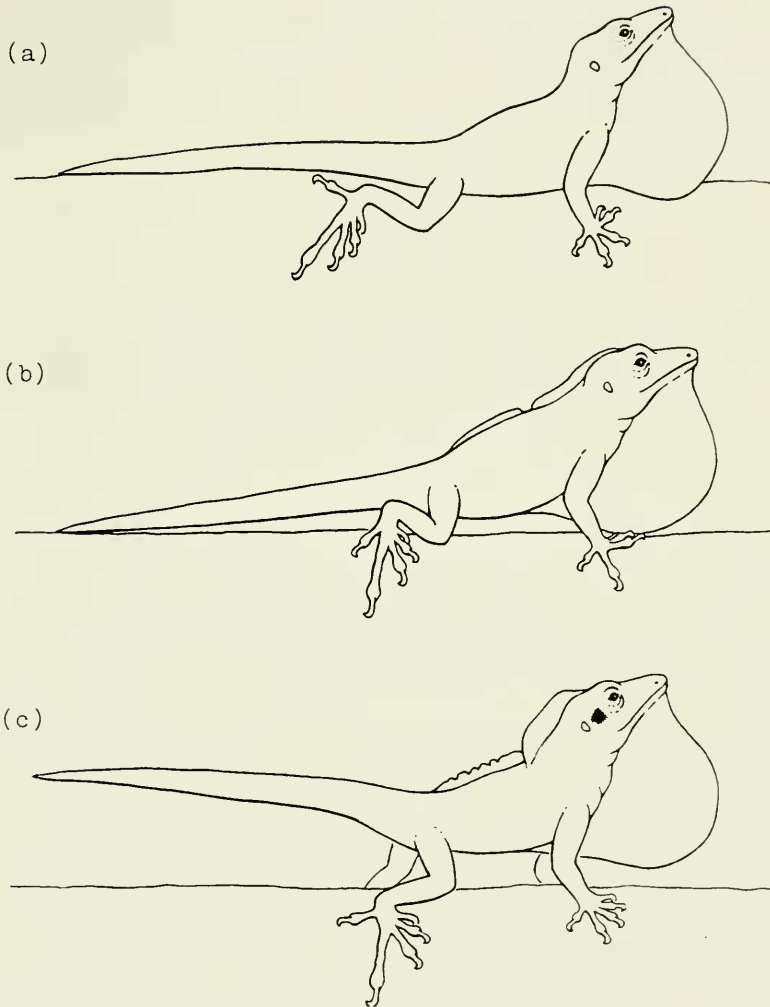


Figure 1. Male *Anolis marcanoii* performing (a) low-level, (b) intermediate, and (c) full elevation displays. Display modifiers shown here, such as crest erection and head spot darkening, were noted in all three display levels, though they were more common in the more aggressive levels.

body and almost completely straightened, while the hindlimbs were pushing up greatly either sprawled out to the side or also under the body. The tail was usually rigidly held straight back or even held higher than the body. The snout was very high, and the dewlap was well off the substrate.

Several particular aspects of the display varied independently of these levels, though in some cases relationships were noted. The most variable, and perhaps most significant, component of the display involved the dynamics of dewlap extension. In general, the degree of extension varied as a function both of time elapsed and intensity of the encounter. The dewlap was usually completely extended and maintained or pulsed (retracted and reextended) to a barely perceptible extent at the beginning of encounters and when a high level of intensity was observed. As encounters progressed into series of alternating exchanged displays, dewlap extension tended to decrease both in extent and duration. Often, the dewlap would only be pulsed out briefly at the end of a series of bobs; the amount of dewlap extended varied similarly, sometimes only revealing a slight bit of the dewlap, and sometimes not at all. If intensity increased, for example as a result of an advance by one of the lizards, dewlap extension would increase in subsequent bobbing.

Anolis cybotes

Anolis cybotes only has one level of dewlap display, comparable to the *low level dewlap display* of *A. marcanoi*. A lizard displayed with its posterior half in contact with the substrate, while its anterior was raised a variable amount by extension of the forelegs (Fig. 2), either out to the side or directly under the body. The snout also was angled upward to a variable degree. On rare occasions, usually when it was on the ground, a lizard displayed with all four legs out to the side, pushing its body up off the ground.

The dewlap was usually extended, at least in the initial bout of displaying, with concurrent head-bobbing. The amplitude, number, and even presence of bobs varied. On occasion, usually later in an encounter, the dewlap was extended and retracted without any head movement at all. As with *A. marcanoi*, sometimes the dewlap was extended and then retracted, while other times it was maintained at full extension.

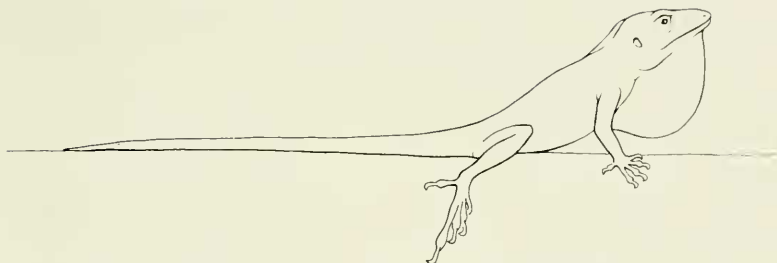


Figure 2. Typical display posture of male *Anolis cybotes*. The forequarters are elevated, but the hindquarters are firmly planted on the substrate. The nuchal crest is occasionally erected more fully, and the dorsal crest is sometimes apparent. The dewlap often is extended more fully.

Head Bobbing

Anolis marcanoi

Though the bobs of the head usually were part of the dewlap extension process, similar to the fanbob of *A. aeneus* (Stamps and Barlow, 1973), in later stages of the encounter, especially when the lizards were alternating displays, the bobs were increasingly emphasized and independent of dewlap extension. A series of 2 to 10 bobs, either of the normal amplitude or greatly exaggerated with several times that amplitude, were performed without dewlap extension, or as a distinct precursor to extension. At other times, the dewlap was pulsed out with exaggerated jerking bobs, similar to the jerkbob of *A. aeneus*. The lizards sometimes bobbed several times at full dewlap extension, with a slight pulse of the dewlap during each bob and slight retractions in between. This usually occurred when the display intensity was high. In several cases, a subordinate lizard raised and lowered its head extremely slowly with large amplitude and no dewlap extension. This was usually repeated several times.

Jenssen (1983) found that *A. cybotes* performed only one stereotyped head bobbing pattern, in contrast to the greater repertoires of other *Anolis* (Jenssen, 1977, 1978). A detailed investigation was not conducted, but from an analysis of the displays of several lizards, it appears that *A. marcanoi* has at least two distinct display types. However, neither the extent of variation nor the degree of stereotypy of the head-bobbing patterns were determined. It is possible

also that *A. marcanoi* has several other head-bobbing patterns that were not discovered. No relationship between level of dewlap display and head-bobbing pattern was found.

In the first pattern, equivalent to the signature display (Stamps and Barlow, 1973; Jenssen, 1978), the head was bobbed once or twice with great amplitude, often with a pause in between bobs, and then rapidly bobbed another 7 to 17 times with the snout remaining elevated (Fig. 3). The dewlap began to expand between bobs six to nine, at which time the bobbing would begin to slow. Several times this display was prefaced with a lowering and raising of the head, akin to, though slower than, the "head-dipping" of *A. cybotes* (Jenssen, 1983). Jenssen (personal communication) pointed out the close similarity between this display pattern and the sole one reported for *A. cybotes*. Only the number of initial large-amplitude bobs—one or two in a *A. marcanoi*, three in *A. cybotes*—distinguishes the two, attesting to the close relationship of the two species. This pattern was observed most often early in encounters, though it was also seen sometimes at high levels of intensity. This description must be considered tentative, however, because it is based on only four displays of three lizards.

A second display, probably functioning as a challenge display (Jenssen, 1978), was often seen late in encounters, especially when lizards were fairly close to each other and alternating displays. It was characterized by a large amplitude dip of the head, a pause, and then three or four rapid low amplitude bobs with the head not quite

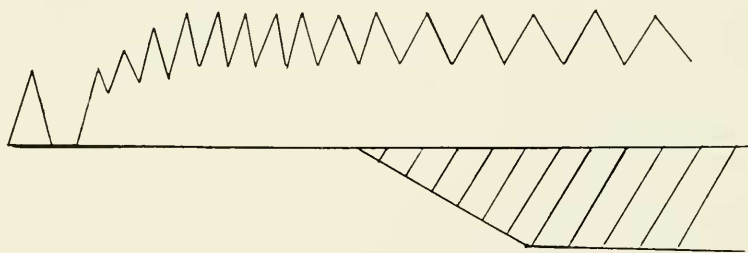


Figure 3. Sample display-action pattern graph of the first head-bobbing pattern of *Anolis marcanoi*. The line represents approximate elevation through time. The shaded region represents dewlap extension through time. This pattern was sometimes preceded by a dip of the head.

dropping back to its original level (Fig. 4). Sometimes, there was a pause after the bob, with the head often not returning to its original level. Usually the dewlap was brought out only at the end of the bobbing sequence, if at all. This description is based on an analysis of nine displays by four lizards. It did seem to be fairly stereotyped, however, and was observed in the displays of many of the other lizards.

Intensity was reflected in the length and magnitude of dewlap display and head-bobbing. More intense encounters tended to have longer displays with greater number of bobs and pulses and greater dewlap extension. The pace of the displays was also faster in more intense displays. If these intense encounters did not immediately progress into more direct aggressive action, however, displays tended to become shorter and less animated, often devolving into the alternating bouts of medium speed bobbing mentioned above.

Anolis cybotes

Because Jenssen has already extensively examined the stereotyped head-bobbing patterns of *A. cybotes*, they were not investigated here. Two distinct methods of bobbing were noted in *A. cybotes*. In one, by far the more common in *A. marcanoi*, the whole head was bobbed, passively moving the dewlap along with it, but without greatly changing its amplitude. This method of bobbing produces the head-bobbing display action patterns so extensively studied in *Anolis*.

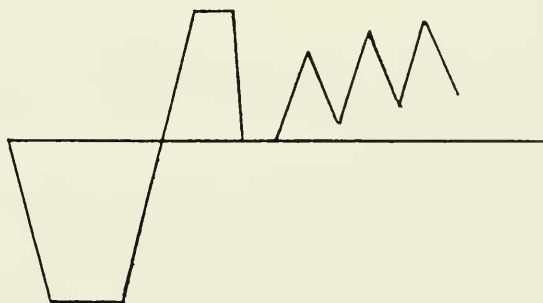


Figure 4. Sample of the second head-bobbing pattern of *Anolis marcanoi*. Though not indicated here, the dewlap was occasionally extended at the end of the display.

By contrast, dewlap bobbing—rarely exhibited by *A. marcanoi*, but commonly performed by *A. cybotes*—primarily involved moving the dewlap up-and-down by raising and lowering the posterior portion of the hyoid, causing a large amplitude change in the dewlap, but moving the head only slightly. This bobbing type was usually preceded by the first type and appeared when the lizard was displaying intensely. Only the first type was involved in dewlap extension.

The quick inverted head bob or “head dip” noted in wild *A. cybotes* by Jenssen was observed on a number of occasions. His observation that head dips were often performed independently of dewlap displays was confirmed, though no long series of head dips, which Jenssen also reported, were noted in these experiments.

Static Modifiers

Several morphological responses—Jenssen’s static modifiers (Jenssen and Hover, 1976; Jenssen, 1977, 1978)—were also indicative of level of intensity, particularly in *A. marcanoi*.

Anolis marcanoi

Both the nuchal and dorsal crests were often erected during displays (Fig. 1b, and 1c). Often, they were erected, retracted, and erected again several times in an encounter. The nuchal crest always appeared before and disappeared after or simultaneously with the dorsal crest. The crests often at first were erected fully, but then retracted to only a fraction of their full size as the encounter continued.

The presence of fully erected crests indicated a high intensity state, but their absence did not imply the converse. When the distance separating the lizards was not great, actions more aggressive than the *full elevation display* were generally accompanied by full crest erection, as were most *full elevation* and some *intermediate elevation displays*. Crests were noted less frequently when the lizards were displaying from across the large terrarium. Lizards that appeared clearly subordinate—indicated by display level, activity, posture, and, retrospectively, by the outcome of the encounter (see below)—were much slower to raise their crests and maintained them generally for a shorter period.

Similarly, the appearance of a dark spot on the side of a lizard's head correlated broadly with intensity. Between the eye and the tympanic opening, a black circular spot slightly larger than the tympanic opening would appear when a lizard was aroused (Fig. 1c). A similar well-defined dark patch with a similar function has been reported for *A. carolinensis* (Greenberg and Noble, 1944; Greenberg, 1977), but in that species the patch is rectangular and directly postorbital without intervening undarkened scales. The appearance of the spot in both species seems clearly a function of arousal; lizards handled during transfer to and from the experimental arena almost invariably exhibited it and often tried to bite. Many other *Anolis* display an irregular darkening in that region when aroused (G. C. Mayer, personal communication; personal observation). Dominant lizards were much more likely to exhibit the spot than subordinate ones, which rarely displayed it except at the highest levels of intensity, and only then when putting up resistance instead of fleeing. As with the nuchal and dorsal crests, black spots were usually apparent, especially on dominant lizards, at high levels of intensity, and sometimes at lower levels, ranging from *low level dewlap displays* to *full elevation displays*. Darkening of the spot almost invariably was preceded by erection—though not necessarily full erection—of the crests. As with crest erection, the spot appeared much more frequently when the distance separating the lizards was not great.

Body orientation and appearance also were important components of the display. Lizards, especially dominant ones, increased their apparent body size several ways. The apparent size of the head was increased by erecting the nuchal crest, engorging the head, and lowering the hyoid apparatus of the throat. Such enlargement is a common aggressive response in iguanids (Greenberg and Noble, 1944; Carpenter, 1967). Presumably, dewlap extension has the same effect of making the lizard appear larger. When retracted, the dewlap remained apparent, ranging in size from a slight rim to a fairly large crescent, making the head region appear larger. The body was also made apparently larger by expansion of the dorsal crest and lateral compression of the body. Subordinate lizards, as well as dominant lizards displaying after winning an encounter (indicated by quiescence or flight of their opponents) rarely attempted to increase their apparent size.

Lizards also attempted to assume a position that would expose the greatest part of their bodies to the other lizard, increasing their apparent size. When both lizards were displaying, the most common position was a parallel alignment, each lizard exposing its broadside to the other. As with many other *Anolis* (e.g., Carpenter, 1965, 1967), when not aligned parallel, one or both lizards (usually the one with less apparent broadside exposure to the other) would turn its head, so that the dewlap when extended would be parallel to the other's head and thus appear as large as possible. Maximizing apparent size was most obvious when one lizard was on a perch while the other was nearby on the ground. In these instances, displaying in an upright position on the branch would not present as large an image as possible to the lizard on the ground. Invariably, the lizard on the branch would display on the side of the branch. The closer the lizard on the ground was to the branch, the greater would be the angle from the vertical of the lizard on the branch. When the lizard on the ground was directly underneath the branch of the other lizard, the latter would arrange itself horizontally, at a 90° angle from the upright. By contrast, a lizard displaying to another lizard also on a perch would always display directly upright on the perch.

Anolis cybotes

As with *A. marcanoi*, several morphological responses were noted as part of the male-male interactive behavior of *A. cybotes*. In the latter species, however, lack of a particular static modifier—or of all static modifiers—did not necessarily correlate with low levels of intensity.

Like *A. marcanoi*, *A. cybotes* possesses both a nuchal and a dorsal crest. The crests appear to be smaller in *A. cybotes* and are fully erected much less frequently. Often, the dorsal crest was visible only as a low ridge along the lizard's back. Crest erection appears to serve the same function in both species, increasing apparent size and indicating heightened level of intensity. In the eight encounters in which dominance could be determined (with *A. cybotes*, dominant lizards could only be determined post facto; dominance could not be determined by the presence of hierarchically higher displays and modifiers as it could with *A. marcanoi*), five of the dominant lizards displayed crest erection. In two of the three other instances, no other

preliminaries to a direct attack occurred. Only two of the eight subordinate lizards displayed crest erection, both in encounters in which the dominant lizard also displayed crest erection.

Anolis cybotes does not have a well-defined circular head spot like that of *A. marcanoi*. It can, however, change skin hue (as can *A. marcanoi*); often, dominant lizards became lighter. An ill-defined darkening of the skin in the postorbital region of the head, where the dark spot in *A. marcanoi* is located, was noted on several occasions, usually when the lizard was aroused by another male or was handled. Only in one lizard, however, was anything approaching a circular spot apparent.

As with *A. marcanoi*, *A. cybotes* attempted to increase its apparent size in various ways. This was observed more often in dominant lizards, though in some cases both lizards attempted to increase their size. Apparent size was increased in several ways, all also exhibited by *A. marcanoi*. Most common, other than dewlap extension, was enlargement of the head. Lizards also increased their apparent size by lateral compression and throat enlargement.

Dynamic Modifiers

Several display modifiers involved moving body parts and thus constituted dynamic modifiers (Hover and Jenssen, 1976; Jenssen 1977, 1978). Instead of bobbing with the head, on several occasions lizards raised and lowered the body by pushing up with the legs, primarily the forelegs. Push-ups have been widely reported among *Anolis* (e.g., Greenberg, 1977; Jenssen, 1979a), and iguanids in general (Carpenter, 1967), but no correlation with intensity was discovered in *A. marcanoi* or *A. cybotes*.

Anolis marcanoi

The *full elevation display* was the most active level of dewlap display. The rear of the body was moved independently in several ways. Most common were push-ups with the rear legs, usually in series of two to six causing the posterior to oscillate greatly, similar to "rearing" observed in *A. opalinus* (Jenssen, 1979a). The precursor of these pelvic push-ups could be seen in several *intermediate dewlap displays* in which the rear legs were raised and lowered slightly as the dewlap was thrust out during head-bobbing. In the *full elevation display*, the lizards also sometimes jumped backwards

several times in rapid succession, forcing the posterior of the body up-and-down in a manner similar to that caused by hind-leg push-ups. Similar behavior in the same context has been noted in male *A. lineatopus* (Rand, 1967). The *full elevation display* was usually only performed in response to a dewlap display or other action by the other lizard in an encounter. Posterior movements were never performed without such provocation.

Head orientation was also related to intensity level. Throughout the dewlap displays, and especially at low intensity levels, lizards changed their head orientation frequently and usually rather slowly. The snout was often pointed at the other lizard, but this action in itself did not seem highly significant. On the other hand, a lizard rapidly turning its snout toward the other, either at the end of a display by the former or during the display of the latter, appeared to indicate a high level of intensity. Generally, pointing occurred during *intermediate* or *full elevation displays* or more intense behavior and was more often performed by the dominant lizard in the encounter. When a dominant lizard rapidly pointed its snout at a displaying subordinate lizard, the latter often ceased its display, retracted its dewlap, and dropped to a less elevated posture.

Anolis cybotes

There was no indication in *A. cybotes* of anything resembling the pelvic push-ups of *A. marcanoi*. The posterior was always stationary and usually firmly on the substrate, though occasionally the entire body was lifted off the substrate.

Pointing with the snout at an opponent was commonly seen in *A. cybotes*, though neither as frequently nor in as defined a manner as in *A. marcanoi*. Several times, a lizard rapidly turned, its snout and even its whole body directed at its opponent, briefly paused, and then leapt at or toward it. The derivation of pointing in *A. marcanoi* may thus be revealed; perhaps pointing in *A. marcanoi* has become ritualized, detached from its original threat of imminent attack. Pointing was never observed by a lizard which would subsequently lose an encounter.

A common action more frequently displayed by *A. cybotes* than by *A. marcanoi* was tilting or cocking the head downward toward an opponent. This often occurred when the lizard was on a branch, looking down upon an opponent on the ground and often was

associated with some movement or action by the other lizard. Though cocking of the head may simply allow better vision of the other lizard's actions, it probably has a communicative function, perhaps as an intention movement, indicating awareness of the other lizard's actions and readiness to respond. *Anolis* also commonly performs this behavior prior to attacking potential prey items (G. C. Mayer, personal communication). Dominant lizards more commonly performed this behavior.

Advancing Behavior

Past the stationary display, the steps of increasing intensity of aggression become more stereotypical, involving movement toward an opponent and threat of or actual attack, though often interrupted by more bouts of unilateral, alternating, or simultaneous dewlap displays. In most cases, the progression to increasing levels of intensity was only stopped by fleeing or quiescence of the subordinate lizard, particularly in *A. marcanoi*, though several times both lizards ceased behaving and assumed less intense postures without either clearly "winning" the encounter.

Anolis marcanoi

Figure 5 presents the flow of advancing behaviors of *A. marcanoi*.

Rapid pointing of the snout toward the other lizard was the lowest level of advancing behavior as well as a display modifier, though it was still usually tied to the interspersed dewlap displays.

Taking one or several steps toward the other lizard is the first overt threat of attack. At close proximity, stepping toward the other lizard threatened imminent attack and often caused the other lizard to cease its display and/or assume a more subordinate position, retreat one or several steps, or seek escape from the encounter.

Also at closer proximity, intent, or at least threat, to attack was indicated by the assumption of a "poised" position. The body was held off the ground with the legs out to the side and appearing ready to spring. The head, enlarged by crest and throat expansion, with the dewlap not usually greatly extended, was tilted somewhat forward and toward the other lizard. Rarely was this position assumed without a subsequent attack. At this time, the lizards were usually in the faceoff position (Carpenter, 1962, 1978), their bodies parallel with heads pointed in opposite directions. When displaying on a

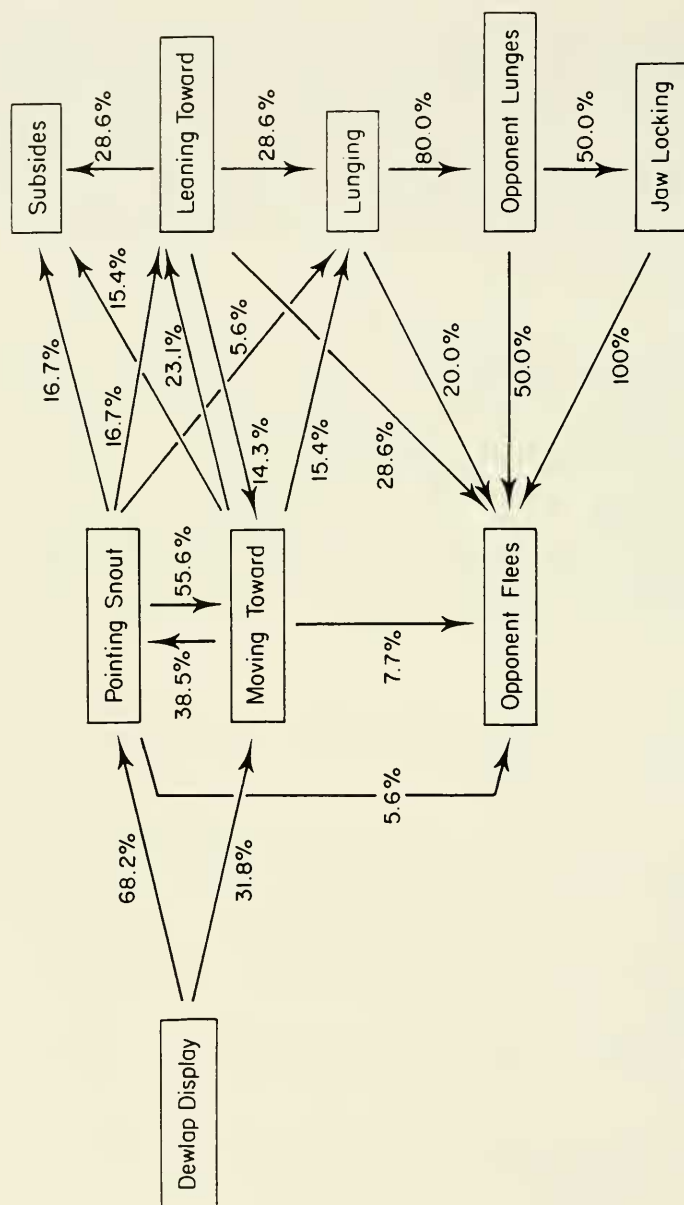


Figure 5. Flow of the behavior of the 22 *Anolis marcanoi* that exhibited advancing behavior. Advancing behavior was always preceded by dewlap display. Dewlap displays and behaviors that occurred more than once—most notably repeated snout pointing—were scored only once. Lunging is only scored for the lizard which initially lunges. Lunges by the second lizard fall into the category of "opponent lunges." Similarly, fleeing is only recorded in "opponent flees." Consequently, output does not always equal input for a box.

perch, this poised position often took the form of a crouch, clearly threatening a jump toward the other lizard. Echelle et al. (1971), in a study of aggressive behavior in nine Costa Rican *Anolis*, noted the assumption of a similar position in males that subsequently attacked their opponents.

Usually following the poised position was an advance toward the rear of the other lizard, culminating in an open-mouthed lunge toward the other lizard's hindquarters. Biting was never observed at this stage. Often the tongue was bunched at the front of the open mouth. Though tongue-bunching is characteristic of aggressive interactions in many *Anolis* species (e.g., Greenberg, 1977), it does not appear to have consistent importance in *A. marcanoi*. Attacking individuals always lunged with mouth open and often kept the mouth open while displaying after lunging. In addition, two lizards opened their mouths in threat displays without immediately lunging afterwards.

The attacked lizard responded either by jumping back and fleeing, or pivoting, usually with a jump backwards, away from the attacking lizard, with its head turned over the shoulder toward the attacking lizard. The two lizards, now in semi-circular positions with heads at opposite ends, displayed at each other, bodies completely elevated off the ground and snouts angled up, with mouths, at least initially, wide open. Occasionally, the attacking lizard continued moving toward the other's rear so that both circled around, maintaining the same relative position. In several instances, the attacked lizard, after displaying, lunged for the other's rear, though in no instance was it successful in driving the former off. In all but two cases, after a sequence of displays, lunges, and circling motions, the attacked lizard fled and attempted to escape the terrarium by running to a distant wall and clawing wildly at it.

In two instances, the two lizards locked jaws for less than two seconds, shaking each other violently, until they released, jumping backwards, with the attacked lizard fleeing. In one of these instances, the attacking lizard chased the other lizard several steps before ignoring it.

In all instances in which the losing lizard fled, the winning lizard continued displaying for up to several minutes. Slowly, the lizard's displays and postures descended the stages of intensity, though they would temporarily reascend if the other lizard came nearby in its

attempts to escape the terrarium. Ultimately, the winning lizard would assume a non-aggressive posture, stretched out on a perch or the ground with its head on the substrate or barely elevated and its rear legs stretched back behind it. The overall effect was to increase its length while decreasing its apparent height. This is the normal resting position of the lizards when undisturbed.

Anolis cybotes

Advancing behavior was progressively ordered to an extent, but not completely (Fig. 6). In the most structured sequences, a lizard performed some display behaviors and then moved towards its opponent, either jumping off a branch or running half or more of the distance separating the lizards. This was usually done at a rapid pace. The advancing lizard then adopted a stalking, "poised" position, somewhat like that exhibited by *A. marcanoi*, but with all four legs out to the side, seemingly prepared to spring, with the long axis of the body pointed directly at the other lizard. This was not always seen, and sometimes a lizard hardly paused between moving toward and actually attacking the other lizard.

The act of biting an opponent was very different in the two species. Encounters involving *A. marcanoi* only resulted in biting when both lizards continued to behave intensely. The sequence of faceoff position-lunging-biting was seen only once in the *A. cybotes* encounters. Instead, most incidents of biting involved very little ritualized behavior. One lizard leapt or ran at the other and bit it behind the head, attempting to pin it to the substrate. Attempts to escape by the attacked lizard often resulted in that lizard carrying the other around on its back. The attacked lizard often was not displaying vigorously and in several cases was trying to escape from the attacking lizard. *Anolis marcanoi* rarely exhibited chasing behavior, but this was common in *A. cybotes*. In the latter species, on occasion, lizards were chased all over the aquarium until they could be cornered and bitten.

Most surprising were two instances in which a lizard, with no preliminaries, ran directly and rapidly at the other lizard, which also had exhibited no aggressive behavior, and bit it behind the head. In both cases, the attacking lizard persistently bit and chased the other lizard until the encounter was ended. This was reminiscent of the "vicious biting attack" termed "abnormal" by Greenberg and Noble

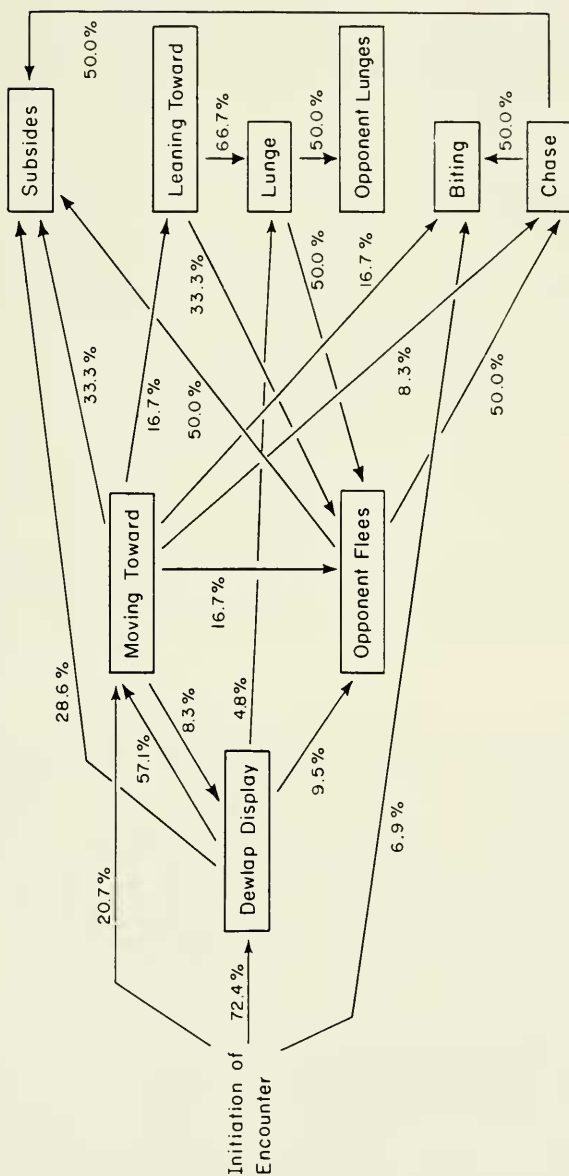


Figure 6. Flow of aggressive behavior of *Anolis cybotes*. See Figure 5 for details of flow chart construction.

in *A. Carolinensis* (1944). This behavior was observed by these investigators in 18 or 800 males, as well as in some females and surgically-altered males.

Submissive Behavior

Anolis marcanoi

As indicated previously, subordinate individuals usually did not posture as intensely as dominant lizards. Dewlap displays were generally less elevated, shorter in duration, less frequent, and often without crests or dark spots. Subordinate lizards also did not as often attempt to enlarge their apparent head or body size.

More submissive behavior generally took the form of staying very low to the ground, with the head elevated little and the snout angled up only slightly, if at all. Carried to the extreme, completely submissive lizards laid completely flat on the ground, appearing as inconspicuous as possible.

At higher levels of intensity, particularly in response to advancing behavior, submissiveness was usually indicated by fleeing the encounter and attempting to escape the aquarium.

Anolis cybotes

One of the most surprising aspects of *A. cybotes*' behavior is the lack of submissive behavior in the lizards that were judged, by the eventual outcome of an encounter, to be subordinate. Unlike *A. marcanoi*, these lizards did not behave less vigorously or aggressively, nor did they necessarily display fewer behaviors connoting higher levels of intensity than the dominant lizard in the encounter. In several cases, the subordinate lizard initiated aggression by moving toward the other lizard. This was never seen in the *A. marcanoi* encounters.

More generally, lizards did not adopt a submissive posture as *A. marcanoi* did. They sometimes moved away or displayed less, but they did not flatten themselves or otherwise appear inconspicuous. Often, a lizard appeared to be trying to escape the aquarium, though neither persistently nor frantically enough to warrant ending an encounter. When this proved futile, the lizard turned back and behaved aggressively again toward the other lizard. Such behavior was rarely exhibited by *A. marcanoi*.

Index of Aggression

In order to quantify levels of intensity in interactions, an index of aggression, similar to that developed for Puerto Rican anoles by Ortiz and Jenssen (1982) was constructed. The index assigns progressively higher point values for actions indicating greater intensity (Table 2). This index, then, can be used to compare quantitatively the level of aggressive intensity of *A. marcanoi* in inter- and intra-specific encounters (Losos, in press). Points for any behavior are scored only once per encounter even though many behaviors are repeated periodically. The score of a lizard in an encounter is the sum of points awarded for behaviors which it exhibited.

The behavior of *A. marcanoi* was progressive, with the less aggressive behaviors preceding the more intense ones. Because this was not the case for *A. cybotes*, no index of aggression could be developed for that species. Occasionally, the actions of *A. marcanoi* during the dewlap display did not necessarily follow a set hierarchy of increasing intensity either. The most notable exception occurred when a lizard, usually at a distance from its opponent, sometimes moved toward the other before pointing its snout rapidly and directly at it.

Table 2. Index of Aggression used to score encounters between adult male *Anolis marcanoi*.

Points	Action or Display Modifier
1	low level and intermediate dewlap display
2	full elevation dewlap display
2	crests erected
3	head spot apparent
3	lifting the pelvic region and/or moving backwards during dewlap display
3	pointing snout rapidly at opponent at conclusion of own display or during opponent's display
4	moving toward opponent (including jumping onto or off of perch)
6	adopting poised position
7	lunging toward opponent
8	locking jaws
8	opponent flees

Several notes on the construction of this index are necessary. Only two levels of dewlap display are scored although three were recognized. The *intermediate dewlap display* stage was considered only slightly more intense than the *low level dewlap display*, and consequently the two were grouped together. Though the nuchal crest is almost always erected before and retracted after the dorsal crest, they are not considered independent behaviors denoting different levels of aggressive intensity. The scores of the lizards agree well with the qualitative evaluations of the 26 encounters. The encounters can be split into four categories based on their outcome: 1. neither lizard supplants the other; 2. displaying and moving toward, one flees; 3. lunging, one flees; and 4. jaw-locking, one flees.

The index well represents the level of intensity of aggression in an encounter (Table 3). Even within particular categories, encounters that qualitatively appeared to be more intense scored higher on the index of aggression. The one discrepancy involves several of the higher scoring encounters in the first category which scored higher than several of the lower scores in the second category. In the former encounters, the dominant lizard was fairly aggressive, adopting the poised position, but then subsiding without forcing the other lizard to flee. In the latter encounters, on the other hand, the subordinate lizard fled immediately after the dominant one jumped down from a perch toward it. These encounters probably would have scored appreciably higher if the subordinate lizard had not so promptly fled; the points awarded for forcing the other lizard to flee were not sufficient to compensate for those lost from the abrupt termination of the encounter. Notwithstanding this one shortcoming, the index appears to satisfactorily evaluate levels of intensity in aggressive encounters.

A second confirmation, with four exceptions, of the index's accuracy comes from comparison of the scores of the lizards judged dominant by their behavior, level of activity, and posture with the scores of those judged subordinate. In no case did the subordinate lizard achieve a higher score than the dominant lizard, while in four instances both lizards received the same score.

DISCUSSION

The male aggressive behavior of *A. marcanoi* appears very similar to that of most other *Anolis* studied, both overall and in particular

Table 3. Results of encounters between male *Anolis marcanoi*.

Encounter	Outcome	Lizards Paired (I.D. Number. Higher Scoring Lizard First)	Dominant Lizard Score/Subordinate Lizard Score	Total	Score
neither	flees	9-18	0/0	0	
		4-12	1/1	2	
		5-9	5/1	6	
		12-2	6/1	7	
		14-16	8/3	11	
		2-13	6/6	12	
		1-7	8/8	16	
		12-6	18/11	29	
		14-3	18/11	29	
		1-10	22/15	37	
		19-5	23/14	37	
displaying,	one flees	3-9	15/6	21	
		1-5	21/4	25	
		3-9	26/6	32	
		2-16	23/11	34	
		13-17	23/12	35	
		13-7	29/14	43	
		5-4	32/18	50	
lunging,	one flees	11-7	35/17	52	
		3-5	39/14	53	
		14-7	39/15	54	
		7-13	33/31	64	
		13-12	36/28	64	
jaw-locking, one flees		16-18	38/30	68	
		19-15	41/29	70	
		9-2	47/26	73	

detail. The progressive nature of increasingly aggressive behavior has long been noted (Greenberg and Noble, 1944; Carpenter, 1967; Gorman, 1968; Jenssen, 1977, 1978; Hover and Jenssen, 1976; Ortiz and Jenssen, 1982). As in the study of five Puerto Rican *Anolis* by Ortiz and Jenssen, the behaviors and modifiers observed generally appeared in a progressive fashion, with some characteristically appearing early in encounters and others appearing progressively later as intensity increased. In most cases there was a clear linear path from one stage to another, though with one major exception, moving forward, which often preceded snout pointing. As noted above,

the ordering of some behaviors and display modifiers depended on distance separating the lizards. At a given distance, behaviors and modifiers generally did not appear prematurely, though many earlier behaviors and modifiers recurred at higher levels of intensity. A comparison of the index of aggression derived for *A. marcanoi* with that derived by Ortiz and Jenssen for Puerto Rican *Anolis* shows great similarity, though the latter is more detailed than the index presented here.

Particular behaviors also resemble those reported for related species. Stamps and Barlow (1973) reported several stages in the dewlap display of *A. aeneus*: fan, fanbob, bob, and jerkbob. Not only were all four stages observed in *A. marcanoi*, but they appeared, very approximately, in equal proportions to those of *A. aeneus*. Crest erection, assumption of the faceoff position, lunging, and jawlocking have been observed in a number of species. Maximizing apparent size by body configuration and orientation is also prevalent among *Anolis* (Jenssen, 1977) and iguanids in general (Carpenter, 1967).

However, there are some differences in the behavior of *A. marcanoi* as well. Pointing with the snout has been reported for only one other species, *A. carolinensis* (and then only at very close range [Cooper, 1977]). *Anolis carolinensis* is also the only species reported to exhibit a well-defined postorbital dark spot. Behaviors noted occasionally in *A. marcanoi*, such as open mouth threats and mouth-smacking, are of greater importance in other species such as *A. opalinus* (Jenssen, 1979a) and *A. aeneus* (Stamps and Barlow, 1973), while actions never observed in *A. marcanoi*, such as tongue protrusion and foreleg lifting, have been observed in many other species (e.g., Rand, 1967; Jenssen, 1979a; Jenssen and Rothblum, 1977; Ortiz and Jenssen, 1982). It appears that as well as having its own stereotyped display-action patterns, each species of *Anolis* has its own behavioral repertoire, sharing some behaviors with other species while possessing a few unique behaviors of its own.

With regard to *A. cybotes*, two related questions merit addressing. Why is the aggressive behavior of *A. cybotes* so much simpler than that of *A. marcanoi*, and, indeed, of all *Anolis* examined? And why is there such little order in the appearance of aggressive behaviors, unlike the highly ordered and progressive pathways of increasing aggression in *A. marcanoi* and other *Anolis*?

Before these questions can be answered, several points of caution must be raised. First, it is possible that the experimental arena was not large enough to elicit the full range and ordering of natural aggressive behavior. Much larger experimental arenas have been used by other investigators (e.g., Jenssen, 1970, 1975; Jenssen and Hover, 1976; Stamps and Barlow, 1973), which was not possible in this case. If this is true, however, it is curious that the same problem did not occur in *A. marcanoi*, which is so similar to *A. cybotes*. Second, the lizards had been in captivity for more than ten months when the last of these experiments were performed. Though most appeared to be in reasonably good health, the long stretch of captive care may have taken its toll on their behavior. The lizards did, however, react quickly and in seemingly normal ways during the encounters; there was just no pattern from lizard-to-lizard or encounter-to-encounter. Third, the encounters involving *A. cybotes* were staged during the winter, a refractory period for males of the species in which their aggressive behavior is diminished in the wild (Jenssen, personal communication). Several *A. marcanoi* tested during the winter (which presumably is the refractory period for this species as well), after the same length of time in captivity, exhibited typical behavior.

Jenssen (1983) argues that the single stereotyped head-bobbing display pattern of *A. cybotes* is a primitive trait with respect to all *Anolis*. The rest of *A. cybotes*' aggressive behavior—dewlap displays, display modifiers, and advancing behavior—are also simpler and less ritualized than that of its sibling, *A. marcanoi*. That this simplicity could not be derived from the more complex behavior of *A. marcanoi*, however, is not clear.

Even if these behaviors are retained primitive ones, the ultimate question, why they have not been expanded and elaborated as in other species, still needs an answer. Jenssen (1983, personal communication) suggests that the determinants of social spacing in *A. cybotes*—a large lizard with large territories, few neighbors, low turnover, and low density—would mitigate against many territorial challenges. Lizards would know their neighbors and rarely challenge them. Intrusion would thus be a matter to be seriously dealt with because interlopers are likely to be lizards without a territory seeking to displace a resident, and because, due to low turnover, available territories would be hard to come by. Consequently, an

intrusion would rapidly result in a fight and elaborate communicatory rituals would be unnecessary. This hypothesis can explain the simplified aggressive behavior of *A. cybotes* compared to that of *A. distichus* (with which it was contrasted by Jenssen), but why such radical differences with its sibling species, *A. marcanoi*, and other truck-ground ecomorphs (*sensu* Williams, 1972), such as *A. cristatellus*, *A. cooki*, *A. gundlachi* (Ortiz and Jenssen, 1982), and *A. lineatopus* (Rand, 1967)? All that can be said is that nothing is known about the spacing and turnover of *A. marcanoi* populations, so direct comparisons with its sibling species cannot be drawn.

One important point can be made about the lack of distinct submissive behavior in *A. cybotes*. In *A. marcanoi*, submissive behavior appeared to have a pacifying effect on the dominant lizard. Only rarely and to a limited extent did a dominant lizard continue to act aggressively toward a clearly submissive opponent. By contrast, submissive behavior elicited no such complacency in *A. cybotes*. Most incidents of biting occurred upon lizards that were not displaying high levels of aggression. Consequently, submissive behavior did not seem to gain any advantage to the lizard displaying it. Rather, perhaps the best defense if escape is impossible is to put up an aggressive front, threatening retaliation in case of attack.

Whether these findings and speculations relate to natural behavior needs to be verified in the field. Studies are needed on the social structure and spacing of populations of both *A. marcanoi* and *A. cybotes* in nature. Furthermore, it is important to find out whether *A. cybotes* does, indeed, need a much greater space between individuals than *A. marcanoi* for naturally progressive behavior to appear.

Other than expanding the general pool of knowledge of *Anolis* behavior, the data here reported hopefully will be of value in investigating the ecological and behavioral interactions of these sibling species. Knowledge of the intraspecific behavior of males of both species will serve as a control with which to compare the results of experiments investigating interspecific male aggressive behavior and the mechanisms of species recognition.

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